

A COMPARISON OF THE PHYSIOLOGY AND ECOLOGY OF THE ESTUARINE ISOPOD *CYATHURA POLITA* IN MASSACHUSETTS AND GEORGIA¹

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The rate of riation and speciation in estuarine species may differ from that of organisms from other environments. Estuaries are characterized by great fluctuations of environmental factors, but since these fluctuations are a permanent feature of the environment, it can be argued that "the aggregate rate of change in the estuarine environment may actually be less than in the geographical province in which it occurs over the same period of time" (Hedgpeth, 1957, p. 695). Simpson (1944) recognized that an organism which adapted to cyclic environmental variations might continue unchanged during climatic changes. This concept indicates that estuarine species may be evolutionarily conservative. Some estuarine forms, such as oysters, gastropod stocks of the Neritacea, and the horseshoe crab, *Limulus*, have persisted for long periods of time relatively unchanged, and may be examples of this evolutionary conservatism (Hedgpeth, 1957).

Species of the isopod genus *Cyathura* are found in estuaries all over the world (Burbank, 1959). Miller and Burbank (1961) have studied a species which is widely distributed along the Atlantic and Gulf Coast seaboard of the United States and have established for it the new combination *Cyathura polita*. They noted intra-specific variations in the apex of the appendix masculinum and in the degree of fusion of the anterior 5 pleonites but did not attempt to correlate these variations with the location of the population which showed them. Burbank and Burbank (1961) have shown that a geographically correlated intraspecific variation occurs in the dorsal chromatophore pattern. They found one type of pattern in animals collected north of the Hudson River, and another in animals collected from New Jersey southward. On the basis of these results they have suggested (p. 263) "... that there might be populations which could be considered distinct races within the species."

The present study was undertaken to evaluate further the variability of the species by comparing two widely separated Atlantic coast populations. A population located in an estuarine meander in Marshfield, Massachusetts, was compared with one in a sandy beach on Sapelo Island, Georgia. Measurements were made of osmoregulatory behavior and oxygen consumption of animals from each population at different temperatures and over a wide range of salinities, and data were collected

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on such ecological features as the habitat niche, population parameters, and the fauna associated with the cyathurans.

MATERIALS AND METHODS

Both populations compared in this study were observed at two times of the year. The Sapelo population was studied throughout the fall of 1961, and was revisited in March, 1962. The Marshfield population was studied in the summer of 1961, throughout the spring of 1962, and again in July and August, 1962. Ecological observations were made whenever the two habitats were visited. Physiological experiments were run on the Sapelo population in the late fall of 1961 and in March, 1962, and on the Marshfield population in the early spring of 1962 and again in July.

Ecological Methods

Habitat observations

The habitat of each population was observed and photographed, and salinity and temperature measurements were made. The salinity was measured by silver nitrate titration. At Sapelo the Mohr method (Barnes, 1959) was used, while at Marshfield, a simplified technique (Barnes, 1959, p. 95) was substituted. The temperature was measured with a Rochester bimetal helix dial thermometer.

Salinity measurements were made in each area at high and low tide. At Sapelo the salinity of the water overlying the beach at high tide and of the seepage water in the beach at low tide was measured. These measurements were made several times in the fall of 1961, and were repeated on March 29, 1962. At Marshfield, the high- and low-tide salinity was measured at the extremes of the cyathuran's range on a spring tide June 30, 1962, and on the following neap tide, July 11, 1962. The temperature of the water in which the cyathurans were living was measured several times during the study of each area.

Population sampling

The dispersion pattern and density of the cyathuran populations were measured by the use of quantitative collecting techniques. At Sapelo Island, sand from 0.1-m² quadrats was sieved through screening of 1.5-mm² mesh, the large animals retained in the screen, and the cyathurans picked out and counted. At Marshfield samples were collected from the bottom of the estuary with a Hayward Dwarf orange peel #1 grab (Burbanck, Pierce and Whiteley, 1956) and the cyathurans sieved out in the same manner. The area of the grab samples varied somewhat but averaged 425 cm². The counts of the cyathurans from each quadrat or grab sample were used to calculate the density and the dispersion pattern of the populations.

The length and sex of each cyathuran collected were determined. The length was measured from the base of the antennae to the tip of the telson. The sex was determined by microscopic examination of the antennae and of the second pleopod, which, in males, carries an appendix masculinum (Miller and Burbanck, 1961). These data were used to calculate the mean size of the animals and the sex ratios in the populations. Since the sex of juveniles cannot be positively determined externally, they were not included in sex ratio calculations.

Faunal association sampling

Animals were collected from each habitat, using the quantitative techniques described above. At Sapelo Island fifty 0.1-m² quadrats were collected within the cyathuran population, while at Marshfield 10 grab samples were taken at each of 10 stations within the range of population.

The animals found in each quadrat or grab sample were identified and counted, and the numerical ranking, density and frequency of each species calculated. The density was determined as the mean number of animals collected per 0.1-m². The frequency was calculated differently in the two areas. At Sapelo it was calculated simply as the percentage of quadrats in which the species was found. At Marshfield, however, most of the species occurred only in a limited part of the range of the cyathurans; therefore their frequency was determined as the percentage of samples in which they occurred compared to the number of samples taken in their part of the range. Thus if a species was collected at only three stations, its frequency was calculated on the basis of 30 samples.

A number of each species were brought back to the laboratory for positive identification and weight analysis. The identifications were validated by taxonomic experts. The ash-free dry weight of each species was obtained by drying several animals at 105° C. for 24 hours, weighing them, then igniting them at 475° C. for 20 minutes, and reweighing. The difference between the weight after drying and the weight after igniting was used as a measure of the ash-free dry weight of the samples. An average specimen weight was calculated and used to obtain an estimate of the ash-free dry weight of the species. Numerical and weight percentages were calculated for each species in the associations and cumulative percentages determined.

Physiological Methods

The cyathurans used in the physiological experiments were collected daily. At Sapelo Island they were collected at mid-tide from an open area of beach near the middle of the population. At Marshfield they were collected at low tide from the bottom of the South River, near a railroad embankment about 300 meters below the upstream limit of the population. About 1000 animals were used in the experiments.

Osmoregulatory behavior

The technique used to determine osmoregulatory behavior of *Cyathura polita* was a modification of a method described by Jones (1941) and Gross (1954). This method measures the concentration of body fluid solutes by determination of freezing point depression.

Cyathurans were acclimated for 24 hours to varying salinity and temperature conditions in fingerbowls which contained 100 ml. of water and a number of 4-mm. glass boiling beads. The fingerbowls were kept in constant temperature water baths throughout the acclimation period. The temperature of these baths was set at 15 and 30° C.; however, the temperature of the water in the fingerbowls was also affected by the room temperature. The experimental temperatures at Sapelo Island were $17 \pm 0.5^\circ \text{C.}$, and $27 \pm 0.7^\circ \text{C.}$; at Marshfield corresponding tempera-

tures were $15 \pm 0.5^\circ \text{C}$., and $27 \pm 0.7^\circ \text{C}$. The water to which the animals were acclimated was collected near the populations, and its salinity was adjusted either by diluting with distilled water or by concentrating with gentle heat. In experiments run at Sapelo Island at 17°C ., salinities were 1.02, 4.0, 8.67, 12.66, 17.1, 20.7, 24.7, 26.2, 28.18, 31.1, and 34.82‰. In experiments run at Marshfield at 15°C . salinities were 1.2, 4.4, 11.42, 17.8, 24.2, 27.6, 29.4, 33.8, and 43.7‰. In experiments run at 27°C ., these salinities were 1.2, 4.65, 11.0, 17.75, 22.0, 27.0, 30.2, and 35.5‰.

Body fluid samples were withdrawn from six randomly selected animals in each acclimated group, and the freezing point depression of the samples determined by comparison with solutions of known freezing point. The raw data on the body fluid freezing point depressions were analyzed to provide a mean and standard error value for each experimental group. These values were then plotted against the salinity to which the animals had been acclimated to provide a graphic representation of the osmoregulatory behavior.

Oxygen consumption

The technique used to measure the oxygen consumption of *Cyathura polita* was a modification of the water bottle method described by Riley and Gorgy (1948), and by Conover (1956). This technique measures oxygen consumption by determination of the amount of oxygen removed from a bottle by an experimental animal in a measured time. It was chosen for use in this study primarily because it does not require that the experimental vessels be agitated during the course of the experiment.

The oxygen consumption experiments were run at temperatures of 15°C . and 30°C ., and at a number of salinities. At Sapelo Island these salinities were 1.02, 4.54, 8.63, 12.48, 17.1, 20.6, 24.21, 29.45, and 35.94‰. At Marshfield they were 1.0, 3.85, 10.4, 15.9, 21.7, 24.2, 27.6, 30.1, and 36.9‰. The animals were acclimated to the experimental conditions of temperature and salinity for 24 hours in fingerbowls similar to those described above.

The experimental vessels were 125-ml. glass-stoppered bottles. In each experiment 8 bottles were flushed with water of the experimental salinity, and randomly selected, acclimated animals of uniform size were introduced into 6 of them. Two bottles were used as controls. All eight bottles were stoppered and placed in a constant temperature bath set at the temperature to which the animals had been acclimated.

The bottles were left in the bath for 24 hours before they were removed and the oxygen concentration of each determined by Winkler titration (Barnes, 1959). The difference between the oxygen concentration in the control bottles and in each experimental bottle was taken as the decrease caused by the respiration of the experimental animal. This concentration difference was used to calculate the volume of oxygen consumed per animal. The ash-free dry weight of the experimental animals was determined by the method described above and used to calculate the oxygen consumption rate in terms of milliliters of oxygen consumed per gram of ash-free dry weight per 24 hours. These data were statistically analyzed to obtain mean and standard error values and plotted against salinity.



FIGURE 1. A photograph of the beach area on Sapelo Island, Georgia, which was inhabited by the southern population of *Cyathura polita*. The photograph was taken at low tide from a point near the lower edge of the intertidal zone. The cyathurans were found living among the sediment particles on the sandy beach.

FIGURE 2. A photograph of the South River, the estuary in Marshfield, Massachusetts, which was inhabited by the northern population of *Cyathura polita*. The photograph was taken at low tide from a point near the upstream limit of the population looking downstream. The cyathurans were found living among the sediment particles on the river bottom.

RESULTS

Ecological Results

The habitats

The habitat of the southern population was a sandy beach located between a steep bluff and a mudflat on the northwestern shore of Sapelo Island, Georgia (Fig. 1). The cyathurans were found in the surface layer of the beach to a depth of 5 centimeters. This layer was a mixture of sand and shell fragments and was underlain by rather impervious muddy-clay. The clay caused water to be retained in the beach at low tide and even on the hottest days the exposed surface remained damp. Many areas of the beach supported stands of the salt marsh grass, *Spartina alterniflora*.

The water which flooded the beach was turbid, well aerated and had wide fluctuations of salinity and temperature. The salinity of the water usually remained relatively constant throughout the tidal cycle, but fluctuated seasonally and during rain storms. During the fall of 1961 the salinity varied between 28.4‰ at high tide and 29.0‰ at low tide. During rainy weather the salinity of the beach water was reduced and during a shower on November 14, 1961, it fell to 25.8‰. The winter and spring rains cause an annual salinity fluctuation and on March 29, 1962, the high and low tide salinities of the beach water were 21.2‰ and 21.9‰, respectively. The temperature range of the water was extensive. During the fall of 1961 this range included a high of 30° C. and a low of 12° C. The turbidity of the water was extremely high throughout the period of study. Usually one could not see more than 15 centimeters into it.

The habitat of the northern population was the South River, a small estuarine meander in Marshfield, Massachusetts. This river becomes recognizable as it leaves the Marshfield World War II Memorial. From this point it runs about 0.5 mile through a fresh-water swamp (Shaler, 1885) dominated by *Typha* species, and about 7.75 miles through a typical salt marsh (Miller and Egler, 1950) dominated by *Spartina alterniflora* and *S. patens*, to a mouth which it shares with the larger North River. The cyathurans were found in the sediments on the river bottom. Their range began about 4.5 miles from the mouth and continued upstream for about 3.5 miles. The bottom of the river was sandy, although larger particles occurred with the sand upstream and smaller particles downstream. Figure 2 is a photograph of a section of the South River.

The water in the South River habitat was characterized by wide daily fluctuations in salinity and wide yearly fluctuations in temperature. The salinity varied from a low of 0.1‰ (low tide at the top of the range) to a high of 28.9‰ (high tide at the bottom of the range). The salinity extremes at the top of the range on a spring tide June 30, 1962, were 2.2‰ at high tide and 0.2‰ at low tide; on a neap tide July 11, 1962, these values were 0.3‰ and 0.1‰, respectively. At the bottom of the range the salinity extremes on the spring tide were 28.9‰ and 9.4‰ and 24.5‰ and 6.6‰ on the neap tide. The yearly temperature range in the habitat was extensive. A low temperature of 8° C. was measured in April, 1962, and a high of 26° C. in August, 1962.

The populations

The individuals in both populations were distributed in irregular, non-random patterns with a high degree of clumping. This clumping was recognized when the collection data were statistically analyzed, and when animals were being collected for physiological experimentation. Large groups of cyathurans were collected from some areas, while superficially similar areas yielded very few.

The sex ratio of both populations was dependent on the time of year. When 47 animals from the Sapelo population were examined on March 30, 1962, 24 were males and 23 were females; when 105 animals from the Marshfield population were examined on May 10, 1962, 49 were males and 56 were females. However, no animals with male characteristics were found when 80 animals from the Sapelo population were examined on November 3, 1961, and only 4 animals with male characteristics were found when 55 animals from the Marshfield population were examined on August 27, 1962. Intermediate periods occurred at intermediate seasons in which there were more animals with female characteristics than with male. A ratio of 32 females to 18 males was found in the Sapelo population on December 11, 1961, and a ratio of 39 females to 11 males in the Marshfield population on July 11, 1962.

Cyathurans collected at Marshfield May 10-16, 1962, were significantly larger than those collected at Sapelo Island on October 6-28, 1961 (mean length 13.3 ± 0.3 mm. as compared with 9.3 ± 0.6 mm.). Male animals collected at Marshfield were significantly larger than females. The lengths of the two sexes were 15.6 ± 0.2 mm. and 12.1 ± 0.3 mm., respectively.

The faunal associations

The data on the animals which were found in the two habitats are presented in Tables I and II. Both associations were made up of a small number of species.

TABLE I
Faunal association, Sapelo Island

Species	No. Coll.	c_e No. Coll.	Cumula- tive c_e	Density No./ 0.1 M.	Fre- quency	Ash-Free Dry Wt.	c_e Dry Wt.	Cumul. Dry Wt. c_e
<i>Nassa</i> (= <i>Nassarius</i>)								
<i>obsoleta</i>	520	52.6	52.6	10.4	84 c_e	9.75	53.1	53.1
<i>Cyathura polita</i>	158	16.0	68.6	3.16	88 c_e	0.23	1.3	54.4
<i>Uca pugilator</i>	109	11.0	79.6	2.18	52 c_e	3.64	19.8	74.2
<i>Gammarus</i> sp.	50	5.1	84.7	1.0	50 c_e	0.06	0.3	74.5
<i>Laconereis culveri</i>	43	4.3	89.0	0.87	48 c_e	0.57	3.1	77.6
<i>Oligochaeta</i>	32	3.2	92.2	0.64	44 c_e	0.42	2.3	79.9
<i>Nereis succinea</i>	22	2.2	94.4	0.52	36 c_e	0.29	1.5	81.4
<i>Littorina irrorata</i>	19	1.9	96.3	0.40	28 c_e	0.30	1.5	82.9
<i>Scoloplos fragilis</i>	17	1.7	98.0	0.34	18 c_e	0.23	1.2	84.2
<i>Mercenaria mer-</i> <i>cenaria</i>	7	0.7	98.7	0.14	14 c_e	2.89	15.7	99.8
<i>Haustorius</i> sp.	6	0.6	99.3	0.12	12 c_e	0.07	0.2	100.0
Dipteran larvae	4	0.4	99.7	0.08	8 c_e			
<i>Pagurus longicarpus</i>	2	0.2	99.9	0.04	4 c_e			

TABLE II
Faunal association, Marshfield

Species	No. Coll.	c_c No. Coll.	Cumula- tive c_c	Density No. 0.1 M.	Fre- quency	Ash-Free Dry Wt.	c_c Dry Wt.	Cumul. Dry Wt. c_c
<i>Scolecopides viridis</i>	860	66.8	66.8	25.3	85%	4.3	33.0	33
<i>Cyathura polita</i>	290	22.4	89.2	6.82	76%	0.6	4.6	37.6
<i>Gammarus tigrinus</i>	100	7.8	97.0	2.4	23%	0.08	0.4	38.0
<i>Nereis virens</i>	11	0.9	97.9	6.47	23%	0.09	0.6	38.6
<i>Anguilla rostrata</i> (elver)	9	0.7	98.6	6.9	13%	1.82	14.0	52.6
<i>Scoloplos fragilis</i>	6	0.5	99.1	6.3	20%	0.04	0.3	52.9
<i>Glossiphonia com- planata</i>	5	0.4	99.5	10.6	30%	0.05	0.3	53.2
<i>Anodonta implicata</i>	3	0.2	99.7	6.4	30%	6.13	47.0	100.0
Dipteran larvae	2	0.1	99.8	4.3	20%			
<i>Crago septemspinosa</i>	1	0.1	99.9					
<i>Mya arenaria</i>	1	0.1	100.0					

Some of these, *Cyathura polita* and *Scoloplos fragilis*, were found in both associations. Others, such as *Gammarus tigrinus* at Marshfield and *Gammarus* sp. at Sapelo, *Nereis virens* at Marshfield and *Nereis succinea* at Sapelo, were closely related to each other. Unidentified dipteran larvae were found in both areas.

Tables I and II make it clear that each association was made up of a few common species and several relatively rare species. Thus in the Sapelo Island association *Nassa* (= *Nassarius*) *obsoleta*, *Cyathura polita*, and *Uca pugilator* made up 79.6% of the animals collected, and in the Marshfield association *Scolecopides viridis*, *Cyathura polita* and *Gammarus tigrinus* made up 97%.

Physiological Results

Osmoregulatory behavior

The results of the experiments on the osmoregulatory behavior of *Cyathura polita* are summarized in Figure 3. The cyathurans from both populations maintained their body fluids hypertonic to their environment at salinities between 1 and about 28‰. However, at salinities between 28 and 43‰ the body fluids were isosmotic with the environmental water.

The level at which *Cyathura polita* maintained its body fluid concentration changed seasonally. In December, the Sapelo animals maintained their body fluid concentration constant at a freezing point depression (Δ_f) of about -1.8° C. In March, this concentration level decreased to a Δ_f between -1.6° C. and -1.7° C. In April, Marshfield animals maintained a constant body fluid concentration at a level between Δ_f of -1.4 and -1.6° C. In July this level rose to a Δ_f over -1.6° C.

Oxygen consumption

The results of the experiments on oxygen consumption are summarized in Figure 4. The cyathurans had a relatively constant oxygen consumption rate over a salinity range from 1 to 37‰. The results of each experiment were compared statistically

to the results of the experiment run at the next higher and lower salinity and, in 29 of the 32 cases compared, no significant difference was found.

No significant differences were found between the oxygen consumption of animals from the two populations. The results of each experiment run on the Sapelo population were compared to the results of the most nearly similar experiment run on the Marshfield population. In 16 of the 18 comparable experiments no significant difference was found.

The oxygen consumption rates for animals from the two populations did not change significantly during the year. No significant differences were found between the rates determined for animals from the Sapelo population in November, 1961, and in March, 1962. Similarly no differences were found in the rates for animals from the Marshfield population in May and July, 1962.

The oxygen consumption of *Cyathura polita* increased at higher experimental temperatures. The mean oxygen consumption rate at 15° C. in the Sapelo popula-

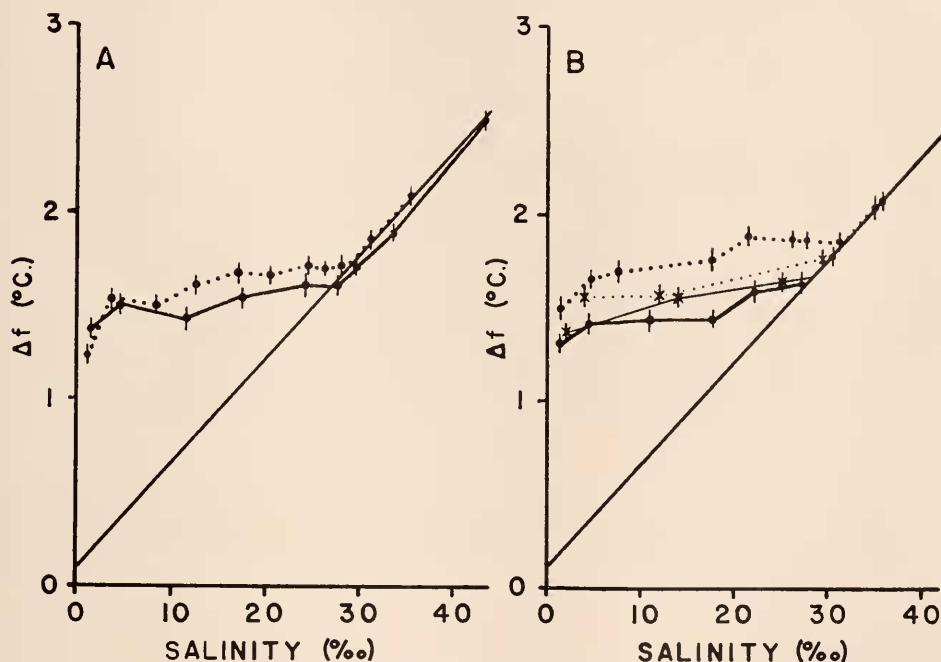


FIGURE 3. The relationship between the freezing point depression (Δf) of the body fluids of *Cyathura polita* and the salinity of the water to which the animals had been acclimated. Each point represents a mean value with vertical lines indicating plus and minus one standard error. The diagonal straight lines represent the depression of freezing point as a function of the salinity of sea water. Graph A shows the results of experiments run at 15–17° C.; graph B, the results of experiments run at 27° C. In both graphs heavy dotted lines represent results of experiments run on Sapelo Island animals in December, 1961, and heavy solid lines represent results of similar experiments on Marshfield animals in April, 1962. In graph B, the light dotted line connecting x's represents results of experiments run on Sapelo Island animals in March, 1962; the light solid line connecting x's represents results of experiments run on Marshfield animals in July, 1962.

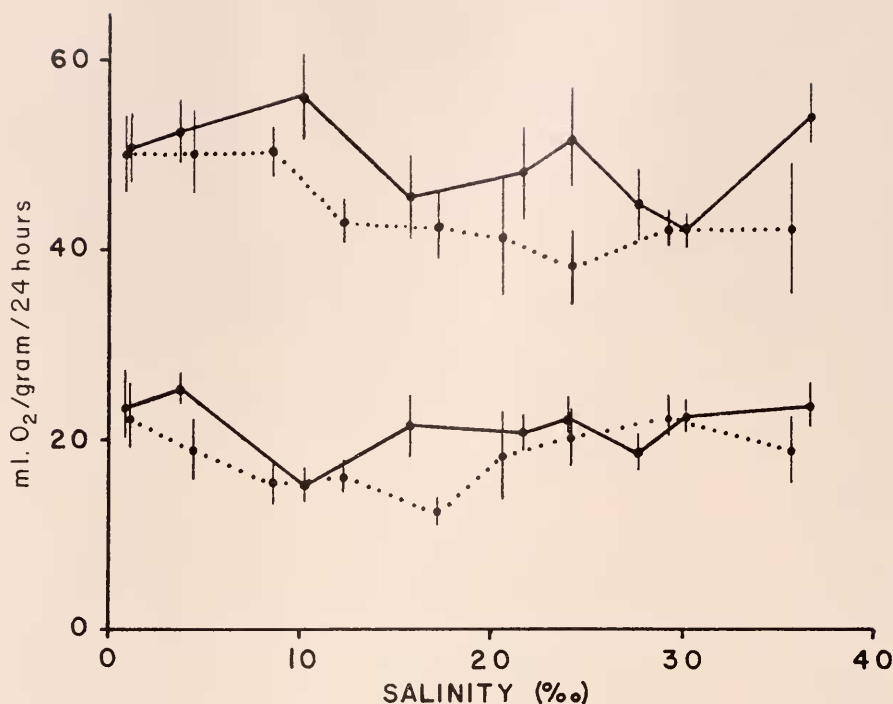


FIGURE 4. The relationship between the oxygen consumption rate of *Cyathura polita* and salinity. The oxygen consumption rate is expressed in milliliters of oxygen consumed per gram ash-free dry weight per 24 hours. Each point represents a mean value with vertical lines indicating plus and minus one standard error. Dotted lines represent results of experiments run on Sapelo Island animals in November, 1961, and solid lines represent results of experiments on Marshfield animals in May, 1962. The upper two lines show results of experiments run at 30° C., the lower two, results of experiments run at 15° C.

tion was 23.5 ml./gram ash-free dry weight/24 hours, and at 30° C. it was 44.6 ml./gram ash-free dry weight/24 hours. The corresponding rates for animals from the Marshfield population were 21.5 and 49.4 ml./gram ash-free dry weight/24 hours.

DISCUSSION

The habitats of the two populations of *Cyathura polita* appeared to be quite different, but closer analysis revealed that they were similar in many respects. Both had sandy sediments, well aerated water and wide fluctuations in salinity and temperature.

Ecological characteristics which were common to both populations were the irregular grouping (Cole, 1946), seasonal changes in sex ratio, and the numerical importance of cyathurans in the faunal associations. The grouped distribution pattern was more fully developed in the Sapelo population, possibly reflecting a subtle interaction of environmental conditions which made some areas of the beach

particularly favorable for *Cyathura polita* (Delamare Deboutville, 1960). The seasonal sex ratio change, currently reported and previously noted by Burbanck (1962), may be a characteristic of the genus since it has been observed both in *C. polita* and in *C. carinata* (Cléret, 1960).

C. polita is an important constituent of many estuarine benthic associations along the Atlantic coast of the United States (Burbank, 1959), has been credited with being the dominant organism in certain specialized situations (Jones and Burbank, 1959), and was one of the three most numerous species at both Marshfield and Sapelo. Yet the numerically important species associated with *C. polita* at one location, such as *Nassa obsoleta* and *Uca pugilator* at Sapelo, are not necessarily the abundant species at another cyathuran habitat (see Table II). Thus, although the fact that 20 of the 21 species found with *C. polita* at Marshfield and Sapelo had previously been reported as associates would suggest that this estuarine isopod is a member of an ecological community, the lack of consistent associates makes it impossible to compile a list of characteristic species for such a community. *Cyathura polita* seems capable of living in a wider range of habitat niches than other estuarine forms and so may be a member of many communities. For example, the one species not previously reported as an associate of *C. polita* but present at Marshfield was the fresh-water mussel, *Anodonta imbecilis*. Many of the streams which Burbanck (1962) has studied on Cape Cod have their upper and lower reaches separated by dams and tidal gates, but the uninterrupted flow of the South River probably allowed cyathurans to migrate into the area inhabited by *A. imbecilis*.

An ecological difference between the two populations was the size of the animals. Those from Marshfield were significantly larger than those from Sapelo. This difference seems to be characteristic of cyathurans and may be similar to the inverse size-temperature relationship found in the fresh-water copepod, *Cyclops vernalis* (Coker, 1934). However, the difference might be a reflection of the unusual habitat of the Sapelo population.

The body fluids of cyathurans from both populations were maintained hypertonic to their environment at low and medium salinities, but became isosmotic with the environment at salinities greater than 28‰. This type of osmoregulatory behavior is common among fresh- and brackish-water organisms (Prosser and Brown, 1961; Lockwood, 1962). It has been described in the shore crabs, *Carcinus maenas* (Duval, 1925; Schlieper, 1929), *Hemigrapsus nudus*, *H. oregonensis*, *Rithropanopeus harrisii* (Jones, 1941); the European river crab, *Potamon edulis* (Duval, 1925); and the isopods, *Mesidotea entomon* (Bogucki, 1932; Lockwood and Croghan, 1957), *Ligia oceanica* (Parry, 1953), and *Asellus aquaticus* (Lockwood, 1959). The results of the present study show that *C. polita* is able to maintain a constant body fluid concentration over a wider range of salinities than many other isopods.

Seasonal variation in body fluid concentration has been found in a number of Crustacea. Lockwood (1960) has studied this relationship on a monthly basis in *Asellus aquaticus* and has found both a gradual variation with season and occasional sharp fluctuations from month to month. Seasonal variations were found in the body fluid concentration levels of *Cyathura polita*.

It is difficult to compare the oxygen consumption rates of different organisms because these rates are affected by many factors, including "activity, temperature,

nutrition, body size, stage in the life-cycle, season, and the time of day, as well as previous oxygen and genetic background" (Prosser and Brown, 1961, p. 157). However, results of different experiments can be compared to illustrate basic relationships (Wolvekamp and Waterman, 1960). Thus the oxygen consumption of *Cyathura polita* resembles that of the isopods, *Porcellio scaber* (Reinders, 1933), *Asellus aquaticus* (Fox *et al.*, 1935), *Armadillidium pallasii* (Müller, 1943), *Oniscus asellus* (Edwards, 1946; Edney and Spencer, 1955), *Armadillidium vulgare* (Edney and Spencer, 1955), *Ligia oceanica* (Ellenby, 1951; Edney and Spencer, 1955), and *Idothea baltica* (Stoicovici and Rosca, 1958). It is lower than that described for such active forms as the amphipod, *Talitrus sylvaticus* (Clark, 1955) and the copepods, *Cyclops leuckarti*, *C. strenuus*, and *Diaptomus graciloides* (Shtcherbakov, 1935), but it is higher than that of such relatively large forms as *Homarus americanus* (Bosworth *et al.*, 1936) and *Uca pugnax* (Brown *et al.*, 1954) or such sedentary forms as *Libinia dubia* (Vernberg, 1956).

The oxygen consumption of *Cyathura polita* remains relatively uniform over a salinity range from 1 to 37‰ (Fig. 4). This relationship is similar to that which has been described in *Artemia salina* females (Gilchrist, 1956), in *Eriocheir sinensis* (Schwabe, 1933), and in the snail, *Theodoxus fluviatilis* (Bielawski, 1960).

The two *Cyathura polita* populations studied seem to be similar physiologically. Animals from both populations had the same type of osmoregulatory behavior and statistically similar oxygen consumption rates. In addition all experimental animals showed a direct relationship between body fluid concentration and temperature, and had oxygen consumption rates which were similar over a salinity range from 1 to 37‰. These similarities are especially striking since the two populations were studied at different seasons. Differences between the populations might be discovered by year-round study of each and by testing reciprocally transplanted animals, but the results of the present study seem to indicate that *Cyathura polita* is a relatively homogeneous species.

Species in which physiological races have developed are characterized by several kinds of variability. Burbank and Burbank (1961) have suggested that variability similar to that described in the ecological races of *Potentilla glandulosa* (Clausen and Hiesey, 1958) can be recognized in *Cyathura polita*. Burbank and Burbank (1961) studied dorsal chromatophore patterns and have shown that some variation occurs within local populations, that populations living under similar environmental conditions may have slightly different patterns, and that northern and southern populations have distinctly different patterns.

The apparent conflict between the results of the present study and that of Burbank and Burbank (1961) can be resolved, however. Clausen (1958) has pointed out that characters which fit a species to its environment are usually homogeneous in comparison with characters which do not. The physiological characters measured in this study were chosen because of their importance in fitting *Cyathura polita* to the estuarine environment. Therefore it is understandable that populations of *C. polita* might have different dorsal chromatophore patterns, but similar osmoregulatory behavior and oxygen consumption rates.

The physiological similarity of the two widely separated *Cyathura* populations may be typical of estuarine organisms. Clausen (1954, p. 477) has suggested that, "natural selection has through geologic ages sifted the naturally occurring (genetic)

variability into workable and balanced combinations of genes and gene blocks that fit certain ecologic niches." Since estuarine niches are characterized by fluctuating environmental conditions, genetic variations which might reduce the tolerance of estuarine organisms to environmental fluctuations would tend to be eliminated by natural selection. This elimination would lead to relatively stable genetic structures. Perhaps the observed evolutionary conservatism of estuarine forms (Hedgpeth, 1957) can be explained not only by the relative permanence of the estuarine environment, but also by the limitations which the estuarine environment puts upon genetic variability. It would be interesting to analyze other estuarine species with wide distributions to see if they show the same physiological homogeneity as does *Cyathura polita*.

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SUMMARY

1. Aspects of the physiology and ecology of two populations of the estuarine isopod *Cyathura polita* have been studied. One of the populations was located in a beach on Sapelo Island, Georgia; the other, in an estuary in Marshfield, Massachusetts. The ecological aspects of the study included habitat observations; analyses of the density, animal size, dispersion and sex ratio of the populations; and investigation of the faunal associations. The physiological aspects included studies of osmoregulatory behavior and oxygen consumption rates.

2. Ecologically, the two populations were similar in a number of respects. They were both found in habitats which had sandy sediments, well aerated water, and wide fluctuations of temperature and salinity. The Sapelo Island population was less dense, and was made up of smaller animals than the Marshfield population, but they both had clumped dispersion patterns and sex ratios which changed seasonally. The faunal associations were limited, and although *Cyathura polita*, and *Scoloplos fragilis*, were the only species found in both areas, others were closely related. *C. polita* was one of the most common animals in both associations.

3. The physiological studies showed that cyathurans from the two populations have similar osmoregulatory behavior and oxygen consumption rates. *Cyathura polita* maintains a body fluid concentration which is hypertonic to its environment at salinities between 1 and 28‰, but which becomes isosmotic with the environment at salinities between 28 and 42‰. The oxygen consumption rate of *Cyathura polita* is similar to that of other isopods. The rate increases at higher temperatures, but does not change significantly over a salinity range from 1 to 37‰.

4. The physiological similarity of the two populations seems to indicate that distinct physiological races have not developed within the species. This physiological homogeneity may be an example of the evolutionary conservatism of estuarine organisms.

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